



NET PRIMARY PRODUCTIVITY OF A WESTERN MONTANE RIPARIAN FOREST: POTENTIAL INFLUENCE OF STREAM FLOW DIVERSION

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ABSTRACT

We estimated aboveground and belowground net primary productivity (NPP) for two reaches of a montane riparian ecosystem in the eastern Sierra Nevada Mountains of California with differing stream flow regimes resulting from varying degrees of stream flow diversion for hydroelectric power generation. Total understory productivity (herbaceous and shrub) was 2.5 times higher ($P < 0.001$) at the high-flow site than at the low-flow site (22.4 and $8.9 \text{ g C m}^{-2} \text{ yr}^{-1}$, respectively). Annual litterfall was also higher ($P = 0.03$) at the high-flow ($235 \text{ g C m}^{-2} \text{ yr}^{-1}$) than at the low-flow site ($180 \text{ g C m}^{-2} \text{ yr}^{-1}$). However, tree and total aboveground NPP, as well as annual soil respiration and belowground NPP, were all statistically similar between sites. Furthermore, total (above- plus below-ground) NPP was statistically similar between sites (903 and $643 \text{ g C m}^{-2} \text{ yr}^{-1}$ for the high- and low-flow sites, respectively). These productivity estimates are, to our knowledge, the first ever reported for a western montane riparian ecosystem. Our results suggest that NPP of montane riparian ecosystems located along gaining stream reaches is only loosely coupled to stream flow, and understory aboveground NPP may be the most sensitive productivity measure to altered stream flow.

Key Words: Net primary productivity, riparian ecosystems, Sierra Nevada Mountains, soil respiration, stream flow diversion.

Riparian ecosystems are among the most heavily disturbed ecosystems in the western United States (US) and have been reduced in area by over 80% since Euro-American settlement (Swift 1984). In the western US, riparian areas currently represent less than 1% of the landscape (Knopf et al. 1988). Although small in area relative to other ecosystem types, the value and influence of riparian areas are greatly disproportionate to their areal extent. For instance, of the 401 species of mammals, birds, reptiles, and amphibians in the Sierra Nevada Mountains of California, over 20% depend directly on riparian habitats, and many others use these areas for foraging, water, cover, shade, and travel corridors. Additionally, 24% of these riparian-dependent species are at risk of extinction (Garber 1996).

In the eastern Sierra Nevada Mountains, many montane riparian ecosystems have been influenced by small-scale hydroelectric facilities constructed primarily in the first quarter of the 20th Century; these hydroelectric plants diverted water away from natural stream channels to facilitate power generation (Harris et al. 1987; Kattelmann 1996). The degree of stream flow diverted ranged from a few percent of the natural discharge to the complete de-

watering of the stream channel (Kattelmann 1996). Typically, water is diverted throughout the entire year. The amount of spring runoff from rapidly melting snow is usually diminished and the timing delayed relative to the undiverted condition (due to water storage facilities associated with the hydroelectric plants), and sporadic releases of water below the diversion, corresponding to peak power demands, commonly occur (Kattelmann 1996). About 20% of the total stream length in the Owens-Mono region has been completely diverted, while almost 90% has been impacted to some degree by diversion (Kondolf 1989). Water diversion reduces stream flow rates and can significantly alter the magnitude, frequency, duration, timing, and rate of change of hydrologic conditions (Poff et al. 1997). Changes in these important hydrologic characteristics can cause stress to riparian ecosystems, resulting in reduced growth (Reily and Johnson 1982), reduced recruitment, and increased mortality (Smith et al. 1991; Stromberg and Patten 1992; Rood et al. 1995). Responses of individual plant species to altered flow regimes will likely affect vegetation community structure (DiSalvo and Hart 2002), resulting potentially in loss of obligate riparian species, invasion by facultative riparian taxa, and reduction in the areal extent of the riparian corridor.

Previous studies have assessed the response of many structural and a few functional attributes of

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western riparian forests to altered stream flow from water diversion. These include: leaf area index, tree mortality, mature tree and juvenile density, radial growth variation, tree xylem water potential, tree leaf stomatal conductance, and water source utilization (Smith et al. 1991; Stromberg and Patten 1991, 1992). However, perhaps the most fundamental characteristic of an ecosystem is net primary productivity (NPP), given that all biological activity, including human activity, is dependent on this process (Whittaker 1975). Indeed, NPP of an ecosystem has been suggested as one of the key attributes for assessing the integrity ("health") of an ecosystem (Costanza 1992; Kolb et al. 1994), as well as the sustainability of management approaches (Christensen et al. 1996). Relatively few investigators have estimated total (i.e., above- and below-ground) NPP of forest ecosystems, and we know of no estimate of above or total net primary productivity for riparian forest ecosystems in the arid, western US.

We assessed the effects of stream flow diversion on the total NPP of a montane riparian ecosystem in the eastern Sierra Nevada Mountains of California. We believe that comparisons of NPP along reaches with different stream flow regimes will improve our understanding of the impacts of water manipulations on these rare and threatened, but vital ecosystems. Given the strong links between stream flow and tree radial growth observed previously in eastern Sierran riparian areas (Stromberg and Patten 1991, 1996; DiSalvo and Hart 2002), we hypothesized that NPP would be higher at sites with higher stream flows. Based on this hypothesis, we also predicted sites with higher stream flows would have concomitantly higher soil C and N pools and rates of soil respiration than sites with lower stream flows.

METHODS

Study Sites and Sampling Design

Our study was conducted on the east slope of the Sierra Nevada Mountains along Bishop Creek, Inyo County, California (Fig. 1). Bishop Creek drains a 180-km² watershed in the rain shadow of the Sierra Nevada Mountains. Mean annual precipitation ranges from about 100 cm (primarily as winter snow) at the upper end of the watershed (ca. 4500 m elevation) to about 15 cm (primarily as winter rain) at the confluence of Bishop Creek with the Owens Valley River (ca. 1350 m elevation). Bishop Creek flows over bedrock and glacial till in its upper reaches, through a steep, glacially carved canyon surrounded by alpine and coniferous forest vegetation. In its mid and lower reaches, the creek is surrounded by Great Basin shrub desert and dissects an alluvial fan before entering the Owens River Valley (Stromberg and Patten 1992). Bishop Creek has a well-defined series of stream flow diversions, which includes three catchment lakes, two

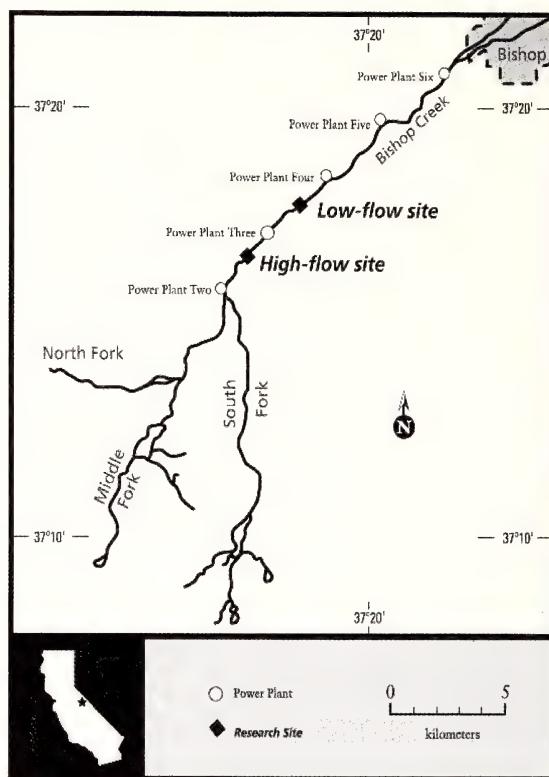


FIG. 1. Location of high- and low-flow sites along Bishop Creek, California. The black squares denote the approximate locations of the two plots assessed at each site. Modified from DiSalvo and Hart (2002).

primary intakes, and five power stations. Stream flows within this watershed have been diverted for nearly a century (Stromberg and Patten 1991), and little information is available on pre-diversion conditions.

Hydrogeomorphological and physiographic factors differ among stream reaches in the mountainous arid western U.S. (Jones and Stokes Associates 1985; Kondolf et al. 1987), and many of the creeks draining the eastern Sierra Nevada Mountains have diverted stream flows (Stromberg and Patten 1992). Hence, we compared riparian ecosystems within the Bishop Creek Watershed along reaches of Bishop Creek with varying degrees of water diversion.

A "high-flow" site (37°17'45"N, 118°32'30"W) and a "low-flow" site (37°18'15"N, 118°31'15"W) were selected for study based on the magnitude of minimum stream flows maintained by Southern California Edison (SCE) within Bishop Creek, as required by the Federal Energy and Regulatory Commission (FERC 1994). Both sites were located along gaining (ground water to stream water) reaches (Space et al. 1989). These two sites were separated by Power Plant 3, and included riparian vegetation growing in a streamside environment. Sites were similar in elevation (1980 and 1910 m

for the high- and low-flow sites, respectively), and were within 1.5 km of each other (Fig. 1). Great Basin shrub desert characterized the upland vegetation at both sites (Chambers Group 1994). Soils at these sites have very low plant-available water storage capacities (Chambers Group 1994) and are members of the Typic Xerorthent, sandy-skeletal, mixed, frigid Soil Taxonomic family (USDA Forest Service 1995). Sites were located within narrow glacial valleys, with an average channel gradient of 11% for the high-flow site and 13% for the low-flow site (Chambers Group 1994). The sites had similar overstories dominated by: *Pinus jeffreyi* Grev. & Balf. (Pinaceae), *Betula occidentalis* Hook. (Betulaceae), *Populus trichocarpa* Torr. & Gray (Salicaceae), and to a lesser extent *Salix* spp. (primarily *S. lasiolepis* Benth. [Salicaceae]). *Pinus jeffreyi*, although not typically considered a "riparian species," is a common member of montane riparian communities of the eastern Sierra, and its occurrence is limited to these environments at lower elevations within these watersheds (Stromberg and Patten 1990; S. C. Hart personal observation). *Pinus monophylla* Torr. & Frém. (Pinaceae) was found at the drier, more upland edges of the riparian corridors. Understories were dominated by *Rosa woodsii* Lindl. var. *ultramontana* (S. Wats.) Jepson (Rosaceae), but also present were *Artemisia tridentata* Rydb. (Asteraceae), *Chrysothamnus nauseosus* Pallas (Asteraceae), and *Purshia tridentata* Pursh (Rosaceae).

Two 50-m long plots were established at each site parallel to the stream, with plot widths extending on both sides of the stream (the stream itself was generally <5 m wide). Plots at each site were not contiguous (separated by at least 50 m), and their location was determined at random with the constraint of matching hydrogeomorphological and physiographic factors of the high-and low-flow sites as closely as possible. The high-flow site was located far enough upstream so that it was not influenced by water impoundment immediately above Power Plant 3. Plot width was determined by the extent of the canopy of obligate riparian vegetation (i.e., *Betula*, *Populus*, and *Salix*) on each side of the stream (Mueller-Dombois and Ellenberg 1974), and thus plot size varied depending upon riparian corridor width (ranging from 20 to 40 m). Plot area (1620–1940 m²) was determined using Trimble GPS units and Pathfinder Office (Pathfinder Office, version 2.0, Trimble, Sunnyvale, CA). The accuracy of these differentially corrected measurements is estimated to be about one meter.

A set of nested subplots (~1 m²) was used for taking soil and litterfall measurements and for sampling adequately all vegetation types within the riparian zone (Bonham 1989). Within each plot, two transects were established, one on each side of the stream and approximately parallel and midway between the stream channel and the edge of the riparian corridor. Subplots were located randomly ei-

ther 5 m towards or away from the stream at 10-m intervals along each transect (n = 10/plot). In these subplots, we measured soil respiration, soil water content, and litterfall (see below). Understory vegetation was sampled within three 0.32 m × 1.25 m quadrats placed side by side and offset 5-m downstream from soil and litterfall subplots (n = 10/plot). Shrubs were sampled within all three quadrats (total area per subplot = 1.2 m²), while herbaceous species were sampled within one of the three quadrats chosen at random (total area per subplot = 0.4 m²).

Microclimatic, Soil, and Stream Measurements

Campbell Scientific (Campbell Scientific Inc., Logan, UT) CR10 dataloggers were used to record microclimatic measurements from 26 May 1999 to 25 May 2000. One datalogger was placed at the upstream plot of the high-flow site and another was placed at the downstream plot of the low-flow site. Dataloggers were located midway between the stream edge and the edge of the riparian corridor. Daily mean soil temperatures were measured using thermistors placed at a 7.5-cm mineral soil depth in environments representative of the plot (n = 4/site). Mean daily air temperature and relative humidity were measured using Vaisala 50Y Temperature and RH probes (Vaisala, Inc., Woburn, MA). Total daily precipitation was measured using an unheated tipping bucket rain gauge placed in an open area outside the riparian corridor (model TE525, Texas Electronics, Inc., Dallas, TX).

Soil volumetric water content was measured approximately monthly from May through November 1999 with a Trace Systems (Soil Moisture Corp., Santa Barbara, CA) time domain reflectometry unit and probes of 0–15, 0–30, and 0–60 cm in length placed adjacent to soil respiration measurements (n = 10 per plot for 0–15 cm and 15–30 cm depths; n = 5 per plot for 30–60 cm depth). Volumetric water contents of the 15–30 and 30–60 cm depths were calculated from the volumetric contents of the 0–15, 0–30, and 0–60 cm probe sets (Kolb et al. 1997).

In May 2000, forest floor (O horizon) mass per unit area (areal density) was estimated for each plot using a 0.093-m² quadrat placed at five of the ten subplots selected at random. Organic matter greater than one centimeter in diameter was discarded, and the remaining material was oven-dried at 70°C. Below the O horizon samples, 5-cm diameter mineral soil cores were removed to a 15-cm depth. Soil samples were air-dried, sieved (=2 mm), ground to a fine powder on a bar mill, and then analyzed for total carbon (C) and nitrogen (N) on an elemental analyzer (Model NC2100, CE Elantech, Inc., Lakewood, NJ). Total soil C and N concentrations were then converted to an oven-dry (105°C) basis using the gravimetric water contents of air-dried soils determined from soil subsamples.

Mean daily stream flow values were obtained from SCE for diversion points directly above our study sites. As part of a riparian monitoring program, SCE has installed gaging stations to determine flows released from power plant locations along Bishop Creek. Read (1994) compared in-stream flow measurements to upstream gaging station stream flows and found that the two measurements were similar and highly correlated.

Aboveground Net Primary Productivity and Leaf Area

Aboveground net primary productivity (ANPP) was estimated as the sum of increases in aboveground standing crop of vegetation plus litterfall (Grier et al. 1989). Biomass losses due to herbivory were not measured; recent studies across a wide range of terrestrial ecosystems suggest that herbivores consume approximately 10 to 20% of ANPP in any given, non-outbreak year (Cyr and Pace 1993; Cebrian 1999). No domestic animal grazing occurred at these sites.

Aboveground herbaceous productivity was assumed to be equivalent to the peak standing crop of the aboveground biomass (Bonham 1989). All aboveground herbaceous biomass was harvested in mid-September, 1999, oven-dried at 70°C, and weighed. Aboveground shrub productivity (stems plus leaves) was estimated at the same time by harvesting and drying current-year growth (Bonham 1989; Grier et al. 1989). Current growth of shrubs was distinguished by differences in color between the current year's and previous year's growth. This approach was verified by marking several stems of each species before the 1999 growing season (Bonham 1989).

Tree productivity was determined for all stems over five cm in diameter at breast height (DBH, 1.4 m) within each plot. We assumed that the contribution from trees with stems < 5 cm DBH to ANPP was relatively small (Whittaker et al. 1974). Stem diameter measurements and increment cores were taken at the end of the 1999 growing season. These data were used in allometric equations found in the literature for each species or a related species to predict aboveground tree biomass in 1998 and 1999. Two increment cores perpendicular to each other were taken at breast height from each tree stem within a plot (a subsample of stems were used with *B. occidentalis*; see below). Increment cores were mounted and sanded following standard methods (Phipps 1985). The 1999 stem radial increment of each core was measured to the nearest 0.001 mm under 20× magnification using an automated measurement system. Radial increments determined on the two cores per stem were averaged and then used to determine the DBH of the stem in 1998 and 1999.

Allometric equations for *P. trichocarpa* and *Salix* spp. were taken from BIOPAK (Means et al. 1994)

and the *P. monophylla* equation from Miller et al. (1981). For *P. jeffreyi*, the equations found in the literature (Means et al. 1994) estimated only tree bole biomass. An allometric equation for bole biomass of *Pinus ponderosa* Dougl. ex Laws. (Pinaceae), developed using data from Gholz et al. (1982) and W. W. Covington (Northern Arizona University, unpublished data), produced nearly identical tree bole biomass values as the equation for *P. jeffreyi* across the range in tree diameters at our sites (two-tailed t-test, $P = 0.35$); additionally, bole biomass estimates were highly correlated ($r^2 = 0.998$, $P < 0.001$), although the *P. ponderosa* equations slightly underestimated *P. jeffreyi* bole biomass (slope = 1.07). Hence, we assumed that the allometries among the other tree components would also be similar between the two species and estimated aboveground tree biomass of *P. jeffreyi* by adding tree bole biomass determined using the equation for *P. jeffreyi* (Means et al. 1994) to foliage and branch biomasses calculated using the equations for *P. ponderosa* (Kaye et al. in press).

No suitable equation was found for *B. occidentalis*, so we developed our own equation based upon stem basal diameter (DBA) using stems ranging in size from 4.6 to 11 cm DBA located adjacent to our plots (total foliar biomass = $\exp(\ln(\text{DBA}) \times 1.591 + 2.861)$, $n = 5$, $P = 0.04$, $r^2 = 0.81$; total stem biomass = $\exp(\ln(\text{DBA}) \times 2.090 + 4.765)$, $n = 5$, $P < 0.01$, $r^2 = 0.97$; DBA in cm, biomass in g). Due to the large number of stems per plot (mean of 592 stems ha^{-1}), a random subsample (approximately 20%) of *B. occidentalis* stems was selected for increment core analysis. A relationship between basal area increment (BAI) per tree and DBA was then derived to estimate tree growth for the 1999 growing season for individuals not measured directly ($n = 72$, $P < 0.01$, $r^2 = 0.11$). Although this relationship is weak, it was the best predictor of productivity from *B. occidentalis*, which comprised only 0 to 3% of the total stem productivity among the plots. *B. occidentalis* stems grow in clumps and other factors (number of stems in clump, stem age) may impact the relationship between BAI and DBA; however, including stem number per tree in the regression equation did not significantly improve its predictive power (data not shown).

Litterfall was collected approximately monthly from 26 May 1999 through 25 May 2000 using circular 0.066 m^2 littertraps (Grier et al. 1989). Littertraps were located within the same subplots where soil measurements were taken, as well as five additional locations in each plot determined at random. Collected litter was sorted by species and plant component (i.e., foliage, flower, wood), oven dried at 70°C, and weighed. Aboveground net primary productivity of trees was calculated by summing the changes in aboveground biomass of tree components between 1998 and 1999 and litterfall estimated over the 1999–2000 period. Biomass and productivity values were converted to a C basis as-

suming that dry biomass was 50% C (Runyon et al. 1994).

We measured leaf area index (LAI) because it frequently correlates with NPP in many forest types (Perry 1994), and previous researchers have found it to be a sensitive measure of structural changes that result from stream flow reduction in western riparian ecosystems (Stromberg and Patten 1996). Projected LAI values were determined by species for each plot using mean specific leaf areas (area per unit mass) measured on these same plots (K. Alstad, Northern Arizona University, unpublished data) and litterfall mass collected in littertraps. Litterfall masses were corrected for reabsorption prior to leaf abscission assuming a 15% loss of mass for *P. jeffreyi* and *P. monophylla* and a 20% loss of mass for the deciduous trees (i.e., *B. occidentalis*, *P. trichocarpa*, and *Salix* spp.; Sedell et al. 1974). *Pinus jeffreyi* and *P. monophylla* LAI values were also adjusted assuming a leaf turnover rate of 0.25/yr (Running 1994).

Soil Respiration and Belowground Productivity

We measured soil respiration monthly from May through November 1999 using a LI-COR 6200 portable photosynthesis system (LI-COR Inc., Lincoln, NE) equipped with an 11.9-l chamber (27.5 cm diameter, 20 cm height; Kaye and Hart 1998). The gas exchange system was calibrated in the field prior to CO₂ flux measurements. Carbon dioxide concentrations were measured over a three-minute period. Carbon dioxide flux was calculated from the linear change in CO₂ concentration in the chamber with time using least squares regression. Ambient air temperature and soil temperature were measured at the time of the respiration measurement. Soil temperature was recorded at a 7.5-cm mineral soil depth or 7.5-cm depth below the ground surface if no mineral horizon was present (i.e., an organic soil profile). Soil respiration measurements were taken within each plot during the same time interval (10:00–14:00 h) on consecutive days; the order by which plots were measured was assigned at random each month. Every month on 10 different subplots, soil respiration measurements were taken every 6 h over a 24-h period to assess diel variation. However, analysis of variance indicated that time of day was not a significant factor in any month or plot ($P > 0.68$; data not shown). Hence, soil respiration measurements taken at a set point during the day were assumed to be representative of the daily flux, and CO₂ fluxes ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) for each subplot were scaled to daily values by multiplying these fluxes by the number of seconds in a 24 h period. Total growing season respiration was determined by integrating daily respiration rates over the growing season (Kaye and Hart 1998).

Soil respiration was not measured during “winter” months (1 January 1999 to mid-April, and in December 1999). Various winter respiration models

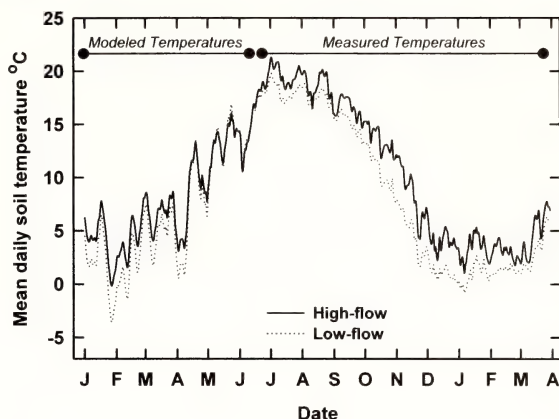


FIG. 2. Mean daily soil temperatures (7.5 cm depth) at the high- and low-flow sites during 1999. Values between May 26 and December 31 were measured using dataloggers and thermistors placed at locations representative of microenvironments at each site ($n = 4/\text{site}$). Values between January 1 and May 25 were modeled using mean daily air temperatures recorded at Bishop, California. The high-flow site had significantly higher soil temperatures ($P < 0.01$, RM ANOVA on ranks).

were tested using combinations of soil volumetric water content, air temperature, and soil temperature under environmental conditions likely reflective of the winter period (i.e., soil temperatures below 16°C and soil volumetric water content [0–15 cm] above $0.06 \text{ m}^3/\text{m}^3$; Figs. 2 and 3). The model that gave the best fit between soil respiration and these environmental conditions was: soil respiration ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) = $\exp [-0.358 + (0.303 \times ^\circ\text{C}) - (0.0121 \times ^\circ\text{C}^2)]$, where $r^2 = 0.437$, $P = 0.002$, and $n = 33$. Soil temperatures were not measured for the entire winter period, so we developed equations that estimated soil temperatures at our sites from air temperatures measured at Bishop, California ($r^2 = 0.92$ to 0.93 , $P < 0.001$). Annual soil respiration was calculated as the sum of measured growing season respiration and modeled winter respiration.

We estimated belowground net primary productivity (BNPP) in our plots from belowground C allocation (BCA) measurements (Raich and Nadelhoffer 1989). Assuming annual changes in soil C pools are small in magnitude relative to loss of C via soil respiration and inputs of C from litterfall (Giardina and Ryan 2002), BCA can be estimated from the equation: $\text{BCA} = \text{soil respired C} - \text{litterfall C}$. Belowground net primary productivity was determined by assuming that root productivity is one-half of BCA and biomass is 50% C (Runyon et al. 1994). Vogt et al. (1998) provides a detailed discussion of the advantages and disadvantages of different methods for estimating BNPP at the ecosystem scale.

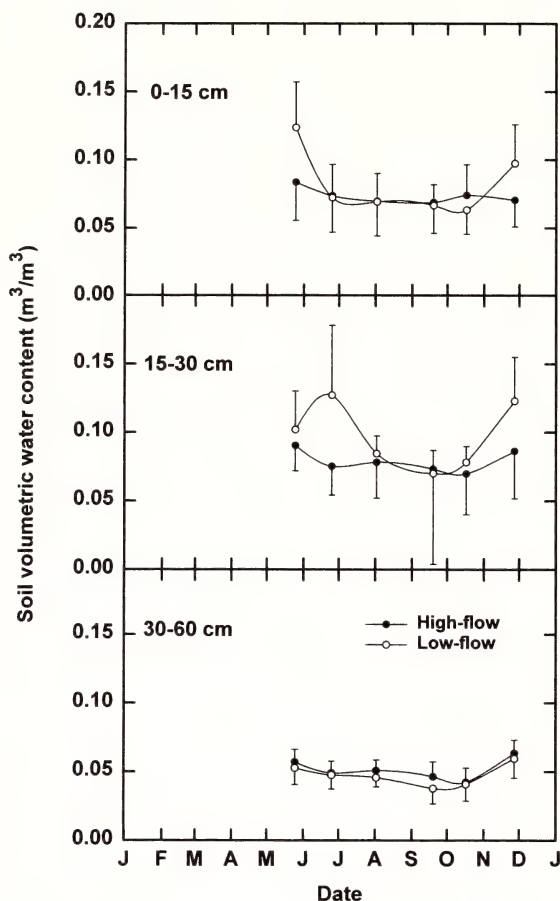


FIG. 3. Mean soil volumetric water content at different soil depths at the high- and low-flow sites during 1999. Vertical bars denote one standard error of the mean ($n = 2$). Error bars for each mean value are shown only in one direction in order to improve clarity. No significant difference in soil volumetric water content was found between sites at any soil depth ($P > 0.05$, RM ANOVA).

Statistical Analyses

Two-tailed t-tests were used to evaluate differences in forest floor mass, mineral soil C and N concentrations, standing biomass, and productivity measures between sites. Repeated measures analyses of variance (RM ANOVA) were used to assess site differences in soil volumetric water content and soil respiration. Repeated measures analyses of variance on ranks were used to test for differences in air and soil temperature, relative humidity, and stream flow between sites because these data violated one of the assumptions of parametric ANOVA.

All analyses were performed with StatView (version 4.5, Abacus Concepts, Inc., Berkeley, CA) except for RM ANOVA on ranks tests, which were performed using SigmaStat (version 2.0, Systat Software, Inc., Richmond, CA). The $P \leq 0.05$ level was used to denote statistical significance.

RESULTS

Median air and soil temperatures were significantly higher at the high-flow than at the low-flow site, but these differences were small in magnitude ($\leq 1.3^\circ\text{C}$; Table 1, Fig. 2). Median relative humidity was lower at the high-flow than the low-flow site, but the magnitude of difference was also relatively minor (3.7%; Table 1). Annual precipitation was 110 mm and 136 mm at the high- and low-flow sites, respectively (Table 1); however, over 90% of this difference occurred during the non-growing season months (data not shown). Annual precipitation at our study sites over the past 74 years, estimated from a correlation between monthly precipitation values measured at our sites and the Bishop Airport, CA (1260 m elevation, <20 km away; $r^2 = 0.81$, $P < 0.001$, $n = 12$), ranged from 71 to 595 mm (mean of 236 mm and CV of 46%).

No significant differences were found in volumetric water content at any depth between sites (Fig. 3). Volumetric soil water content was low ($<14\%$) in all soil depths in these skeletal, coarse-

TABLE 1. SELECTED SITE CHARACTERISTICS OF RIPARIAN SITES ALONG BISHOP CREEK, CALIFORNIA. ^a Data shown are modeled values for 1 January 1999 to 25 May 1999 and measured values for 26 May 1999 to 31 December 1999 (see text). ^b Precipitation values are for 26 May 1999 to 25 May 2000; annual precipitation was not tested for difference between sites due to lack of replication. ^c Probability values for tests of differences between sites using RM ANOVA on ranks for air and soil temperatures and relative humidity; parametric RM ANOVAs were used for forest floor mass and soil carbon (C) and nitrogen (N) concentrations.

Characteristic	Site		
	High-flow	Low-flow	P value ^c
Median daily air temperature ($^\circ\text{C}$) ^a	16.5	15.2	<0.001
Median daily soil temperature ($^\circ\text{C}$) ^a	15.3	14.4	<0.001
Median daily relative humidity (%) ^a	25.5	29.2	<0.001
Annual precipitation (mm) ^b	136	110	—
Mean forest floor mass (g/m^2)	25.6	17.4	0.21
Mean soil C concentration ($\text{g C}/\text{kg}$)	21.8	26.5	0.71
Mean soil N concentration ($\text{g N}/\text{kg}$)	0.88	1.1	0.69

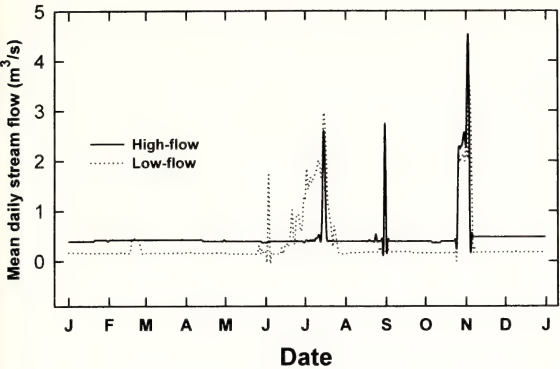


FIG. 4. Mean daily stream flow at high- and low-flow sites during 1999. Daily stream flow at the high-flow site was significantly higher than stream flow at the low-flow site ($P < 0.001$, RM ANOVA on ranks).

textured soils. No significant differences existed between sites for forest floor mass, mineral soil C concentration, or mineral soil N concentration (Table 1).

Median daily stream flow (discharge) for the high-flow site for 1999 was $0.39 \text{ m}^3/\text{s}$ and was significantly higher than the low-flow site stream flow of $0.17 \text{ m}^3/\text{s}$ (Fig. 4). Annual stream flow over this period was $16 \times 10^6 \text{ m}^3$ and $11 \times 10^6 \text{ m}^3$ at the high- and low-flow sites, respectively. Median daily stream flow during the growing season (May–Oct.) was significantly higher at the high-flow site ($0.40 \text{ m}^3/\text{s}$) than at the low-flow site ($0.17 \text{ m}^3/\text{s}$; Fig. 4). Total growing season stream flow was $8.1 \times 10^6 \text{ m}^3$ and $7.5 \times 10^6 \text{ m}^3$ at the high- and low-flow sites, respectively. However, most of these differences in stream flow between sites occurred because of differences in base flows rather than peak flows (Fig. 4).

Mean ANPP of herbs was $7.5 \text{ g C m}^2 \text{ yr}^{-1}$ at the high-flow site and $3.6 \text{ g C m}^2 \text{ yr}^{-1}$ at the low-flow site, but these differences were not statistically significant ($P = 0.623$). Mean ANPP of shrubs was $14.9 \text{ g C m}^2 \text{ yr}^{-1}$ at the high-flow site and $5.4 \text{ g C m}^2 \text{ yr}^{-1}$ at the low-flow site, but these values also were similar statistically ($P = 0.288$). Shrub productivity at both sites was dominated by *Rosa woodsii* var. *ultramontana*, however, this species contributed less to shrub ANPP at the high-flow site (69%) than at the low-flow site (88%) site. Above-ground NPP of the second most prevalent shrub species, *Artemisia tridentata*, represented approximately 10% of total shrub production at both sites and was not statistically different between sites. However, total understory (herbaceous and shrub combined) ANPP was 2.5 times greater at the high-flow site ($22.4 \text{ g C m}^2 \text{ yr}^{-1}$) than at the low-flow site ($8.9 \text{ g C m}^2 \text{ yr}^{-1}$), and this difference was highly significant (Table 2).

Mean aboveground tree biomass at the beginning of 1999 was similar statistically at the high-flow

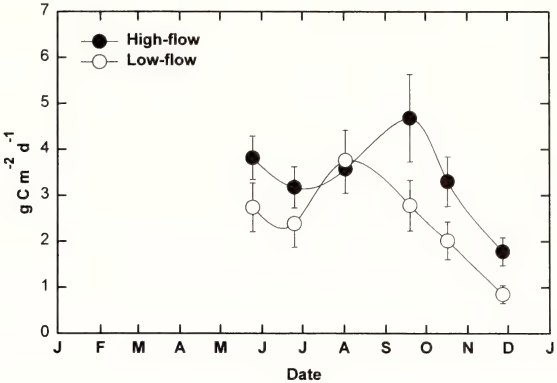


FIG. 5. Mean daily soil respiration from high- and low-flow sites during 1999. Vertical bars denote ± 1 standard error of the mean ($n = 2$). Soil respiration rates were statistically similar between sites ($P = 0.09$, RM ANOVA).

site (11.6 kg C/m^2) and the low-flow site (7.25 kg C/m^2 ; Table 2). The majority of aboveground tree biomass was contributed by the species *Pinus jeffreyi*, which represented 94% and 87% of the total tree biomass in the high- and the low-flow sites, respectively. No significant differences in above-ground tree biomass were found between sites for any individual tree species with the exception of *Populus trichocarpa*, which had significantly higher aboveground biomass at the low-flow site (Table 2). The annual change in aboveground tree biomass (ΔB) between 1998 and 1999 was also dominated by *P. jeffreyi* at both sites, where growth of this species comprised 80 to 85% of total ΔB ; however, both total ΔB and ΔB of *P. jeffreyi* alone were similar statistically between sites (Table 2). The only statistically significant differences in ΔB between sites for individual tree species occurred for *Pinus monophylla* and *P. trichocarpa*, where ΔB was higher at the low-flow site (Table 2).

Annual litterfall at the high-flow site was 235 g C/m^2 , which was significantly greater than at the low-flow site (180 g C/m^2 ; Table 2). *Pinus jeffreyi* contributed the most litterfall at both sites (51% and 44% of the total for high- and low-flow sites, respectively), and litterfall from this species was significantly higher at the high-flow than at the low-flow site. No other tree species had significantly different litterfall between sites (Table 2). Wood, shrub, and unidentifiable material contributed approximately 17%, 3%, and 1%, respectively, to the total annual litterfall at both sites (Table 2; not all data shown). Leaf area comparisons between sites and among tree species generally followed a similar pattern as annual litterfall (Table 2).

Mean tree ANPP ($\Delta B + \text{litterfall}$) was statistically similar between sites for all individual species and for total tree ANPP (Table 2; total tree ANPP not shown). Furthermore, mean total ANPP (sum of herbaceous, shrub, and tree ANPP) was statisti-

TABLE 2. LEAF AREA, ABOVEGROUND BIOMASS, AND COMPONENTS OF NET PRIMARY PRODUCTIVITY AT HIGH- AND LOW-FLOW SITES ALONG BISHOP CREEK, CA. ^a Means $\pm$ 1 SE; n = 2. ^b Probability values for a significant difference in that component between sites (two-tailed t-tests).

Component	Site		P value ^b
	High-flow	Low-flow	
1998 Projected Leaf Area Index (m ² /m ²)			
<i>P. jeffreyi</i>	1.8 ± 0.2	1.1 ± 0.1	0.06
<i>P. monophylla</i>	0.17 ± 0.16	0.12 ± 0.07	0.80
<i>P. trichocarpa</i>	1.6 ± 1.3	3.1 ± 0.4	0.40
<i>B. occidentalis</i>	1.0 ± 0.4	1.1 ± 0.1	0.82
<i>Salix</i> spp.	0.11 ± 0.03	0.02 ± 0.00	0.06
Total	4.7 ± 1.0	5.4 ± 0.2	0.52
1998 aboveground tree biomass (g C/m ²)			
<i>P. jeffreyi</i>	10,940 ± 1420	6308 ± 781	0.10
<i>P. monophylla</i>	59.5 ± 38.4	353 ± 120	0.15
<i>P. trichocarpa</i>	193 ± 7	309 ± 22	0.04
<i>B. occidentalis</i>	453 ± 156	230 ± 89	0.34
<i>Salix</i> spp.	0.0	54.2 ± 51.0	0.40
Total	11,640 ± 1230	7254 ± 917	0.10
Change in tree biomass 1998–1999 (g C/m ²)			
<i>P. jeffreyi</i>	193 ± 57	127 ± 37	0.44
<i>P. monophylla</i>	1.2 ± 0.3	4.2 ± 0.6	0.04
<i>P. trichocarpa</i>	8.2 ± 0.3	10.1 ± 0.2	0.03
<i>B. occidentalis</i>	26.2 ± 6.8	12.1 ± 4.0	0.22
<i>Salix</i> spp.	0.0	1.7 ± 1.7	0.41
Total	228 ± 50	155 ± 40	0.38
Leaf litter production (g C m ⁻² yr ⁻¹)			
<i>P. jeffreyi</i>	122 ± 9	53.4 ± 2.3	0.02
<i>P. monophylla</i>	4.8 ± 4.6	3.3 ± 2.0	0.79
<i>P. trichocarpa</i>	37.9 ± 30.3	61.0 ± 7.4	0.53
<i>B. occidentalis</i>	26.1 ± 8.0	32.5 ± 3.2	0.53
<i>Salix</i> spp.	4.5 ± 1.0	0.8 ± 0.1	0.07
Total tree leaf litter production	195 ± 19	151 ± 5	0.15
Total litter production	235 ± 0.3	180 ± 9	0.03
Total aboveground NPP (g C m ⁻² yr ⁻¹)			
<i>P. jeffreyi</i>	314 ± 66	181 ± 35	0.21
<i>P. monophylla</i>	6.0 ± 4.9	7.5 ± 2.5	0.81
<i>P. trichocarpa</i>	46.0 ± 30.6	71.1 ± 7.2	0.51
<i>B. occidentalis</i>	52.3 ± 1.2	44.6 ± 7.2	0.40
<i>Salix</i> spp.	4.5 ± 1.0	2.5 ± 1.7	0.42
Herbaceous and shrub	22.4 ± 0.2	8.9 ± 0.5	0.002
Total aboveground	468 ± 30	324 ± 37	0.09
Soil respiration (g C m ⁻² yr ⁻¹)	1126 ± 213	828 ± 59	0.31
Belowground NPP (g C m ⁻² yr ⁻¹)	434 ± 107	319 ± 25	0.40
Total ecosystem NPP (g C m ⁻² yr ⁻¹)	903 ± 137	643 ± 11	0.20

cally similar between the high-flow site (468 g C m⁻² yr⁻¹) and the low-flow site (324 g C m⁻² yr⁻¹; Table 2).

Mean soil respiration rates measured between May and November 1999 were similar statistically between the high- and low-flow sites; however, soil respiration rates were consistently higher at the high-flow site, except for the August sampling period when stream flow was actually higher at the low-flow site (Fig. 4). Annual soil respiration was estimated as 1126 and 828 g C/m² in the high- and low-flow sites, respectively, and did not differ between sites (Table 2). Mean BNPP values calculated from C balance were statistically similar be-

tween sites (434 and 319 g C m⁻² yr⁻¹ for the high- and low-flow sites, respectively; Table 2). Mean total NPP (ANPP plus BNPP) of the entire ecosystem was also statistically similar between the high-flow site (903 g C m⁻² yr⁻¹) and the low-flow site (643 g C m⁻² yr⁻¹; Table 2). The ratio of BNPP to total NPP was close to 0.5 at both sites (Table 2).

DISCUSSION

Tree growth has been shown to be tightly coupled to stream flow in some riparian forests of the western U.S. (Stromberg and Patten 1990, 1991, 1992, 1996; DiSalvo and Hart 2002; Galuszka and

Kolb 2002). Stream, soil, and ground water may all serve as sources of water for trees in these ecosystems depending on the relative availability of the source and the rooting habit of the tree species (Smith et al. 1991). Reservoirs and diversions that alter stream flow reduce high flow periods (i.e., spring snow melt) that recharge aquifers and soils. Over the life-span of the riparian vegetation, stream flow reduction via diversion could reduce NPP by decreasing water availability to plants within the riparian corridor. Over the longer term, stream flow reductions caused by water diversion could reduce NPP by altering plant community composition, reducing leaf area index, or both.

Contrary to our hypothesis, most of the productivity measures we assessed (i.e., change in above-ground tree biomass, total ANPP, BNPP, and total NPP) were not higher at the site with higher stream flows in 1999. However, annual litterfall (due to higher litter production by *Pinus jeffreyi*) and understory (herbaceous plus shrub) ANPP were significantly higher at the high-flow site. We speculate that a shallower rooting distribution of the understory compared to the overstory trees contributed to the lower ANPP of the understory at the riparian site with a lower stream flow.

If this is indeed the mechanism responsible for the difference in understory productivity between the sites, then we would have expected to find a difference in the availability of water in surface soils at the two sites. However, our monthly measurements of soil water content showed no significant differences between the high-flow and the low-flow sites at any soil depth. Monthly measurements of soil water content, particularly near the surface, may be insufficient for documenting soil water dynamics in the coarse-textured, skeletal soils of these riparian sites because of their low capacity to store water (USDA Forest Service 1995); low water storage capacity should lead to relatively rapid changes in soil water content in response to changes in stream flow and ground water depth (Brady and Weil 2001). Other possible mechanisms that may account for the observed differences in understory ANPP between sites include depth to ground water, soil nutrient availability, solar irradiance, and temperature.

Unfortunately, we were unable to directly measure ground water depth due to the prohibitive cost of drilling wells in the rocky soils found at our sites. However, Read (1994) examined ground water depth from 1991–1993 along a gaining and a losing reach of Bishop Creek within a few kilometers of our sites. She found that average depth to ground water was approximately 0.7 to 1.2 m despite variation in stream flows from less than 0.14 m³/s to more than 1.70 m³/s. Hence, it is unlikely that there were any large differences in depth to ground water between the two sites. Although we did not assess nutrient availability directly, the similar total C and N pools in soils at these sites

do not support differences in nutrient availability as a possible mechanism. Furthermore, we measured total irradiance at the meteorological stations installed at each site and found no significant difference (data not shown). Hence, it is unlikely that differences in photosynthetically active radiation contributed to the patterns we observed. Air and soil temperatures were slightly higher at the high-flow site, and tree growth is weakly correlated to maximum air temperature at these sites (DiSalvo and Hart 2002). Hence, higher temperatures and a longer growing season (Fig. 2) could have also contributed to the differences in understory ANPP between sites that we observed.

Stream flows during the growing season may better represent the relationship between water supply and the NPP of riparian ecosystems than total annual flows. Stromberg and Patten (1991) found that growing-season stream flow correlated better with annual tree-ring growth of *Populus* spp. than did annual stream flow within the Bishop Creek Watershed. Although 1999 annual stream flow at the high-flow site was 30% higher than at the low-flow site, stream flow during the 1999 growing season was only 8% higher. Furthermore, growing-season stream flows in 1999 at both these sites were higher than the average flows estimated between 1969 and 1988 (ca. 8.6×10^6 m³/yr; Stromberg and Patten 1991). If stream flow is a significant factor controlling NPP in these ecosystems, we would expect much larger differences in NPP between our sites during low-flow years when the disparity between sites in growing season stream flows would likely be magnified.

Differences in stream flow between the two sites were due primarily to higher base flows at the high-flow site. It is unclear in these montane riparian ecosystems if higher peak flows or higher base flows are more important in regulating NPP. Higher peak flows may result in greater recharge of soil water farther away from the active stream channel, but higher base flows likely provide higher sustained soil water availability near the stream channel. We speculate that higher base flows are likely more important within the upper reaches of the Bishop Creek Watershed because of the relatively narrow riparian corridors and low soil water storage capacities. Future studies need to experimentally determine how differences in stream flow characteristics alter NPP in these and other riparian ecosystems with regulated stream flows, particularly given these two characteristics are largely under the control of water managers.

Because this was an observational study that was also unreplicated at the “treatment” (i.e., stream diversion) level, we cannot unambiguously attribute any differences between sites to stream flow diversion. The vast majority of the trees at both these sites were established post-diversion (DiSalvo unpublished data); hence, current stand structural differences observed between sites (Table 2) are prob-

ably the cumulative result of decades of altered stream flows. Although ANPP of *P. jeffreyi* was not significantly higher at the high-flow site, litter production (which often is a good index of ANPP; Perry 1994) was higher. Hence, we speculate that the lack of a significant difference in ANPP between sites is a combined result of a small seasonal difference in stream flows between these sites in 1999, as well as lack of statistical power in our experimental design (see below). Indeed, previous research at these and similar sites have shown that radial growth of many of the tree species (including *P. jeffreyi*) is correlated to stream flow across years (Stromberg and Patten 1990, 1991, 1996; DiSalvo and Hart 2002); like litterfall, radial growth should be positively correlated to ANPP (Perry 1994).

We used estimated changes in standing aboveground biomass of *P. jeffreyi* between the high- and low-flow sites during the decade of the 1990s to evaluate this hypothesis. Differences in growing season stream flows between sites during this period on average were much greater than in 1999 (DiSalvo and Hart 2002; DiSalvo, unpublished data). This retrospective analysis was possible because we measured diameter increment over the previous decade in this species, and the allometric equations used to predict biomass required only DBH (DiSalvo and Hart 2002). We found that changes in aboveground standing biomass (ΔB) averaged 29% higher at the high-flow site than at the low-flow site over this decade (RM ANOVA, $P < 0.001$). Because *P. jeffreyi* contributed the vast majority of the ANPP at both sites in 1999 (Table 2), this result suggests that ANPP also was higher in the high-flow site over this period. We stress the need for replicated experimental manipulations of stream flow in riparian ecosystems for establishing unequivocally the relationship between stream flow diversion and NPP in these and other riparian ecosystems.

To our knowledge, the estimates of NPP given in this paper are the first ever reported for a western montane riparian ecosystem, and we know of only one other study (Clawson et al. 2001) that has previously estimated the belowground NPP of any riparian ecosystem worldwide. Aboveground productivity values (ranging between 288 and 499 g C m⁻² yr⁻¹ among our plots) were within the lower end of the range of those reported for other riverine systems, which span from 324 g C m⁻² yr⁻¹ to 1068 g C m⁻² yr⁻¹ (Brinson et al. 1990; Clawson et al. 2001). Lower ANPP values for arid, high-elevation western riparian ecosystems are likely due to a combination of factors, including highly variable stream flows, low and highly variable precipitation, short growing seasons, low relative humidity (causing reduced stomatal conductance when water is limiting), and the low water storage capacities and nutrient availabilities of the poorly developed soils they occupy (Smith et al. 1991; Adair and Binkley 2002). Nevertheless, stand-level leaf area indices

were moderate relative to values reported for upland temperate deciduous and evergreen forests (Landsberg and Gower 1997; Waring and Running 1998).

Our calculated estimates of BNPP (which includes all plants) were similar statistically between sites. Some studies in upland forests suggest that the relative allocation of total production belowground is higher in sites with greater belowground resource constraints on production, such as water stress and low nutrient supply (Keyes and Grier 1981; Gower et al. 1992; Runyon et al. 1994; Haynes and Gower 1995; Landsberg and Gower 1997; Raich 1998). Our results do not support this hypothesis given that BNPP:total NPP ratios from our sites (≈ 0.5) were at the high end of the range reported for these upland forests (0.2 to 0.6), and our assumption that at least one belowground resource, water, would be more readily available in riparian than in upland forests. In one of the few studies that have assessed both BNPP and ANPP in a riparian forest, Clawson et al. (2001) reported that the BNPP:total NPP ratio did increase as water availability declined in a floodplain forest of the southeastern U.S.. However, they also reported surprisingly low BNPP:total NPP ratios in these floodplain forests across all sites (from 0.03 to 0.13). Apparently, riparian forests may exhibit even greater variation in the patterns of C allocation across sites than has been found for upland forests.

Analyses of ecosystem functional attributes, like NPP, can be difficult due to the high-degree of spatial and temporal heterogeneity inherent within ecosystems, as well as the number of ecosystem components that need to be assessed to generate system-level measures. We conducted power analyses (two-tailed t-test, $P < 0.05$; Zar 1998) to estimate how many plots per site would be required to detect significant differences in 1999 for some of the productivity measures that did not show differences (assuming that differences did indeed exist). Based on these analyses, we would have needed 5 plots per site for ANPP, 25 plots for BNPP and 9 plots for total NPP in order to detect a significant difference between these sites. This result clearly illustrates the difficulty of measuring belowground and total NPP in these ecosystems. We believe, like many other researchers (Gregory et al. 1991; Muller et al. 2000), that ecosystem-level studies of riparian zones provide a rigorous ecological basis for evaluating ecosystem health, identifying management objectives, evaluating current management practices, and the development of future management plans. However, our results suggest that the only productivity measure likely to provide a sensitive, cost-effective index for evaluating the effect of stream flow diversion on western montane riparian areas is understory ANPP.

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